THE ANATOMY OF CERCIDIUM TORREYANUM AND PARKINSONIA MICROPHYLLA

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The palo verdes, *Cercidium Torreyanum* and *Parkinsonia microphylla*,[1] are small trees, common in the sandy washes of the southwestern deserts. Typically xerophytic, they appear in leaf only for a short time in early summer, but later in the season, although the branches are leafless, the trees are still conspicuous by the vivid greenness to which they owe their common name.

When working on the lignification of the xylem fibres of *Parkinsonia*,[2] I was unable to find in literature any connected, detailed account of the structure either of *Parkinsonia*, or of the closely related genus *Cercidium*, and I have therefore outlined the salient anatomical features of these two typical southwestern forms.

Cercidium Torreyanum (Wats.) Sarg.

Examination of a transverse section of the stem of *Cercidium Torreyanum* (pl. I, fig. 3) reveals such generally accepted xerophytic characters as heavily cutinised epidermis, sunken stomata, hypodermal water-storage layer, cortical chlorenchyma, abundance of oil-containing idioblasts throughout the parenchyma, and strong development of fibres in the vascular cylinder. The various tissues in the stem and the root will first be considered in detail. Thereafter the anatomy of the leaf and the seedling will be briefly outlined.

Stem. In the young stem the epidermis is one cell deep, and the cells are heavily cutinised. Hairs, generally unicellular, are present on the youngest stems. The cells retain the power of division and the epidermis increases in circumference during secondary thickening. The cells also divide tangentially, and thus a multiple epidermis results in the older twigs. The cuticle appears cracked on the surface, but it remains nevertheless a continuous layer, due to the activity of the underlying epidermal cells.

The stomata are sunken, and are arranged in parallel vertical lines along the stem. The long axes of the stomata are at right angles to the axis of the stem. Projecting ridges of cutin, characteristic of xerophytes, protect the stomata. The layer of cutin may extend through the stomatal aperture and line the roof of the respiratory chamber (pl. I, figs. 1, 2). The epidermis remains as a living functional layer for many years, and

[1] Jepson, W. L., Manual of the Flowering Plants of California. 1925.
[2] Scott, F. M., Am. Journ. Bot. (in press).

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cork formation, generally speaking, is confined to the older trees. Here and there, however, near the branch crotches, and elsewhere intermittently on the younger branches, perhaps in response to insect or other wound stimulus, isolated patches of cork may occur. The development of the cork begins, as usual, near a stoma, and in the process of cork formation the hypodermal cells are eventually sloughed off.

Beneath the epidermis lies a layer of hypodermal tissue, consisting of thin walled, unlignified, water containing cells, devoid of chloroplasts. This hypodermis is, in the young stem, one cell deep, but tangential division may take place later in some of the larger cells. The layer is interrupted at the stomata, and since the cells of the hypodermis vary in size, the hypoderm-chlorenchyma junction appears as a sinuous line (pl. I, fig. 3). The cells of the hypodermis in fresh material are clear and colorless, and appear to be filled with a mucilaginous material. Microchemical tests indicate also the presence of traces of sugar, oil, and of protein material.

Collenchyma is generally present in younger stems, but is not more than two or three cells thick.

The photosynthetic chlorenchyma is made up of several layers of palisade-like cells, with the usual intercellular spaces (pl. I, figs. 1, 2). Starch and oil are abundant throughout this tissue, the latter appearing to impregnate the chloroplasts, and being also distinguishable in the form of droplets of varying size in the protoplasm. The chlorenchyma is bounded on the inner face by a single layer of colorless cells, presumably containing water and mucilage, inside of which appears a heavy pericyclic ring of lignified elements, alternating groups of fibres and stone cells (pl. I, fig. 2). In the youngest stems the fibres alone are present.

In the parenchyma of *Cercidium,* including the hypodermis, calcium oxalate is abundant at various times throughout the year. It occurs generally in the form of large rosette crystals, but tabular crystals may also be observed. Tannin is noted occasionally in the same tissues.

The most striking feature in the vascular cylinder, at all seasons of the year, is the abundance of starch throughout the xylem. In young twigs the vascular bundles are separate, and later they are united in a continuous cylinder as in a typical woody dicotyledon. The component elements in the phloem are fibres, sieve tubes, with terminal and lateral sieve plates, companion cells, and a certain amount of phloem parenchyma. The xylem is made up of tracheal tubes, reticulate and border pitted, and of characteristic substitute fibres (pl. I, fig. 4, f_1, f_2). The medullary rays are as a rule one cell wide and from six to twenty cells high. The seasonal rings are well marked, since the few tracheal elements are laid down only at the beginning of the growing period. It was noted that the growth rings are often somewhat asymmetric in the younger branches, but the distribution of this asymmetry has not been further investigated. The substitute fibres in *Parkinsonia* have been described in some detail by the writer,[2] and the fibres of *Cercidium* appear to be similar. During the active growing season, the cambium cuts off a series of xylem and phloem elements in the usual way, and the course of development of the xylem substitute fibres may easily be followed. Thickening of the cell wall is followed by lignification, and thereafter starch grains accumulate in the fibres, eventually blocking the lumen completely. The substitute fibres remain alive, and in some cases appear to be multinucleate. A very marked difference in wall thickness serves to distinguish spring and summer substitute fibres.

From the standpoint of causal anatomy a curious feature is the occurrence of a strand, crescent shaped in transverse section, of unlignified cells ensheathing the protoxylem tip of the vascular bundle. For reasons unknown this strand escapes the ubiquitous lignification which takes place not only in the xylem, but also in the central core of pith. The latter is composed of typical parenchyma, in which lie scattered groups of fibres. Both are completely lignified in relatively young twigs.

Root. The heavy development of cork in the older root is another typically xerophytic character seen in the anatomy of *Cercidium.* The component cells of the root tissues are similar to the corresponding elements already described in the stem. Characteristic, as before, are the starch containing substitute fibres which form the bulk of the solid xylem cylinder. The tracheal tubes, as is general in roots, are wider in lumen than those occurring in the stem. Oil is abundant in the cortical cells. The development of the root will be outlined below in the description of the anatomy of the seedling.

Seedling. The seed coat of *Cercidium Torreyanum,* like that of *Parkinsonia,* to be described in detail later, is extremely hard, but germination of the seeds may be speeded up by soaking them three to four hours in concentrated sulphuric acid, and washing thereafter overnight in running water. After such treatment the radicles appear as a rule within forty eight hours.

The seedlings were examined at various stages of growth, and the development of the vascular system, including the transition region, was traced. The accompanying diagrams of transverse sections of the axis, cut at various levels in a seedling 12.8 cm. long, serve to illustrate the main points (pl. I, figs. 5–10).

In a seedling at this stage the cotyledons are green and somewhat fleshy and the plumule is beginning to develop. The hypocotyl-root junction, in this case approximately coincident with the transition region, is marked by a circular ridge. The epidermis and the surface layers of the cortex on the hypocotyl become suberised very early, in this differing from the surface of the developing plumule. Secondary roots appear at this time in the upper part of the root.

In regard to the anatomy of the young seedling, it may be seen that the tissues near the root tip are still undifferentiated. In the region of elongation, a procambial cylinder is defined, while further back, in the root hair zone, the differentiation of the vascular system and of the endodermis is apparent. The root is tetrarch, and the protoxylem elements, as in other similar roots, are laid down at the inner margin of the food conducting cylinder, constituting the "alternate phase" of development (pl. I, fig. 5). Passing upwards, lignification now extends tangentially, and a more or less complete cylinder of xylem thus arises, the "intermediate" phase, which is maintained up to the level of the root-hypocotyl ridge (pl. I, figs. 6, 7). At this point the additional metaxylem elements are perforce laid down outside the xylem cylinder, and the superposed phase of the typical stem is now realized (pl. I, fig. 8). This is accompanied, in a seedling of this size, by the usual separation of the vascular bundles, as they pass upward to the cotyledons and the developing plumule (pl. I, figs. 9, 10). At the level of development of the superposed phase, that is, in the transition region, the endodermis, typical of the root, comes to an end, and at the same time the development of the phloem fibres, typical of the stem of *Cercidium,* begin to appear (pl. I, figs. 7, 8).

It is thus seen that the seedling *Cercidium* resembles fundamentally the tetrarch seedlings of the widely divergent genera *Ricinus*[3] and *Chilopsis*.[4]

In *Cercidium,* an accessory endodermis is occasionally present in the developing root. The radial walls of this layer bear the usual very heavy thickenings, which appear in transverse section as semicircular ridges. The exact details of the occurrence or absence of this layer were not determined.

Leaf. The leaves, as already noted, appear after the winter rains and persist, as a rule, for a very short time. In them, as might be expected, xerophytic adaptations are not at all evident. The pinnae are rather thin, and consist of one or two layers of palisade, and three or four layers of spongy mesophyll tissue. Cuticle is present on the surface of the epidermal cells, but is not markedly thickened as in the stem. Stomata are present on both upper and lower surfaces of the leaflets, and the guard cells lie almost level with the surface. Hypodermal cells are

[3] Scott, F. M., and Sharsmith, H. H., Am. Journ. Bot. 20: 176–187. 1933.
[4] Scott, F. M., Am. Journ. Bot. (in press).

developed only beneath the midrib, and intermittently beneath the submarginal veins. These cells resemble the hypodermal cells of the stem, and like them may contain a certain amount of oil. Between the palisade and the spongy mesophyll tissue, thick-walled spherical idioblasts occur, clearly defined by their content of oil.

Parkinsonia microphylla Torr.

In general habit *Parkinsonia microphylla* differs from *Cercidium* in length of leaf, the rachis bearing from 15 to 25 pairs of leaflets, in contrast to the three or four pairs of the other genus. The leaflets are shed before the rachis, and the latter persists for a time as a functional photosynthetic organ. While no study has been made of the movements of leaflets of the two genera, a problem of undoubted ecological interest, it is observed that in *Parkinsonia* in cultivation the pulvini of the leaflets are actively functional, and the leaflets fold at night parallel to, and along the upper surface of the rachis.

The anatomy of the stem and root, of the seed coat, and of the leaf will be briefly outlined.

Stem. In structure the stem is essentially similar to the stem of *Cercidium,* with multiple epidermis, horizontal guard cells, xerophytic hypodermal layer, chlorenchyma, pericyclic fibres and stone cells, xylem consisting in the main of starch-containing substitute fibres and relatively few pitted or spiral tracheal tubes, and a pith in which scattered groups of fibres occur. Ergastic substances—starch, oil, tannin, and calcium oxalate—are likewise similar in occurrence.

Root. The anatomy of the root does not differ in any essential from that of *Cercidium.* The xerophytic layer of cork is equally developed in both genera.

Seedling. In regard to the seedling axis, the diagrams which illustrate the structure in *Cercidium* serve equally well to illustrate *Parkinsonia.*

Seed Coat. The structure of the seed coat also is similar in both the palo verdes. The seed coat, as has been indicated by the somewhat drastic treatment necessary to speed up germination, is extremely hard and is of highly complex structure. When a section of the ripe seed coat is cut, five layers may be distinguished, three of which are well defined, while the other two appear as crushed and insignificant tissue (pl. I, fig. 11). The protective outer coating is made up of columnar cells, thick-walled and heavily cutinised, particularly towards the inner border. A light line of unknown function is present and is indicated in the figure (pl. I, fig. 11, i). This is followed by a lignified zone, ten to twenty cells deep, of fibres variously oriented. Oil is abundant in this tissue, as may be seen with the use of Sudan III. This stain also serves to delimit the third layer of the seed coat, a narrow zone of somewhat crushed and thin-walled cells, heavy staining of which gives the impression of a cuticular layer separating the fibrous layer from the underlying mucilage cells (pl. I, fig. 11, ii, iii, iv). The latter resemble mesophyll cells in their branched form, and in their loose grouping. Traces of oil are still obvious in the cell contents. During germination the mucilage layer expands enormously as the measurements in the diagram indicate. The walls very soon disintegrate into a formless mass. The innermost lining of the seed coat, layer five, consists of somewhat irregular crushed cells with slightly cutinised cell walls (pl. I, fig. 11, v).

Leaf. The rachis, as has been noted, bears a large number of deciduous leaflets, and as may be expected from this deciduous habit, no marked xerophytic characters are developed in the pinnules. In transverse section the leaflet differs from that of *Cercidium* mainly in the lack of the occasional spherical oil-containing idioblasts. The anatomy of the rachis and of the pulvinus are, however, distinctive features.

Three leaf traces enter the leaf base, but as they enter the pulvinus they merge to form an incomplete cylinder (pl. I, fig. 12). This flattens as it passes into the rachis, and gives off the numerous lateral veins which constitute the vascular supply of the leaflets. The pulvinus in transverse section is circular in outline, and, as usual in such structures, the vascular and the mechanical tissues are concentrated near the center of the axis. The mechanical sheath surrounding the vascular tissue in the pulvinus consists of thickened fibres with walls of cellulose while in the rachis the corresponding fibre walls are heavily lignified. Chlorenchyma tissue with rather thick walls forms the main bulk of the pulvinus tissue, bounded by a single layer of epidermal cells. No hypodermal tissue is present.

The flattened elliptical leaf-like outline of the rachis is evident in plate I, figure 13. The tissues are similar to those in the photosynthetic stem, although differing in the degree of development. Thus the multiple epidermis of the older stem is represented by a simple epidermis one cell thick, and the hypodermis likewise is only a single layer in depth. Stomata are present on both the upper and the lower surfaces, and the occurrence of palisade chlorenchyma on both surfaces produces a bifacial structure. The distribution of the vascular and the mechanical tissue in relation to the chlorenchyma and the central layer of mesophyll is illustrated in the diagram.

Summary and Conclusions

The palo verdes, *Cercidium Torreyanum* and *Parkinsonia microphylla,* similar in their general vegetative habit, are also strikingly similar in their typically xerophytic structure.

1. The stem in both is photosynthetic, and is characterised by a heavily cutinised epidermis, with sunken stomata transverse in position. Beneath the epidermis lies a large celled hypodermis, which, however, is interrupted opposite the stomata, so that the latter lead directly into the respiratory chambers, the intercellular spaces in the cortical chlorenchyma.

2. The usual ergastic substances, starch, an abundance of oil, and occasionally tannin, are present in these tissues. At certain times also calcium oxalate in the form of rosette crystals, or infrequently in the form of tabular crystals, fills practically the entire lumen of the hypodermal cells.

3. When the cork eventually develops in the older stem, it is subepidermal in origin; as it increases in thickness, the hypodermis sloughs off.

4. The vascular cylinder is delimited by a pericyclic ring of fibres and stone cells. The xylem is heavily lignified throughout, and is distinguished by the abundance of starch-containing substitute fibres.

5. As is the case in xerophytes generally, the root is protected by a well developed layer of cork; otherwise the only distinctive feature of the root appears to be the inconstant occurrence of a secondary endodermis.

6. In the seedling the development of the vascular system including the transition region follows the tetrarch pattern of *Ricinus* and *Chilopsis.*

7. It is only in the leaves of the two genera that marked anatomical differences occur. The leaflets, however, are essentially similar, in that they are deciduous in both, and do not possess any marked xerophytic characters. On the other hand, the rachis of *Parkinsonia,* with its conspicuous basal pulvinus and leaf-like photosynthetic structure, is distinctive. The fibrous sheath surrounding the vascular strand of the pulvinus consists of unlignified fibres, which grade into heavily lignified elements in the rachis.

A survey of the anatomy of the palo verdes thus raises certain points of interest in regard to the metabolism of these xerophytic forms. Seasonal growth, that is a period of active photosynthesis and food storage, is indicated by the occurrence of annual rings. Yet in the material examined at different times throughout the past two years, no significant variation in the amount of reserve starch was observed. Is this starch, then, to be considered merely as unavailable excess material; or would it under more favorable conditions be utilised to an appreciable extent?

In addition to starch, oil is present as a reserve material, both in the protoplasts of the parenchyma cells, and impregnating the walls of xylem and phloem lignified elements. The actual content of oil and water of the living cells presumably varies from season to season, but whether this variation runs to the extent of a phase reversal in the colloidal system remains a question.

The conditions necessary for the extensive deposition of calcium oxalate in the hypodermal cells were not determined.

The intensive lignification of desert plants is well known, and implies, perhaps, that loss of water in the cell wall is at least one condition necessary for the process of lignification. The structure of the pulvinus and the adjacent rachis, where lignified and unlignified elements grade into each other, is therefore of interest from the standpoint of causal anatomy.

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Explanation of the Figures. Plate I

Cercidium Torreyanum

Fig. 1. Longitudinal section of stem, showing stoma and surrounding tissues: *c,* cuticle; *e,* epidermis; *h,* hypodermis; *s,* stoma; *r c,* respiratory chamber; *cr,* cortex (camera lucida, ×150).

Fig. 2. Transverse section of a similar stem: *g c,* guard cell; *p f,* phloem fibre (camera lucida, ×150).

Fig. 3. Transverse section of stem (diagrammatic), distribution of tissues: *ph,* phloem; *cm,* cambium; *x,* xylem; *pt,* pith; *pt f,* pith fibres.

Fig. 4. Transverse section xylem cambium junction (camera lucida, ×150): *m r,* medullary ray; *t t,* tracheal tube; f_1 and f_2, thickened and less thickened fibres.

Figs. 5 to 10. Transverse sections of the seedling axis at various levels showing the development of the vascular system and the transition region: *r h,* root hair; *end,* endodermis; *px,* protoxylem; *mx,* metaxylem; *f,* fibres.

Parkinsonia microphylla

Fig. 11. Transverse section of seed coat: layers i, ii, iii, iv, v (camera lucida, ×150). The measurements of the various layers are indicated in microns.

Figs. 12, 13. Transverse section of pulvinus and rachis, respectively: *s f c,* sheath of unlignified fibres; *s f l,* sheath of lignified fibres; *pal,* palisade; *v b,* vascular bundles; *mes,* mesophyll.

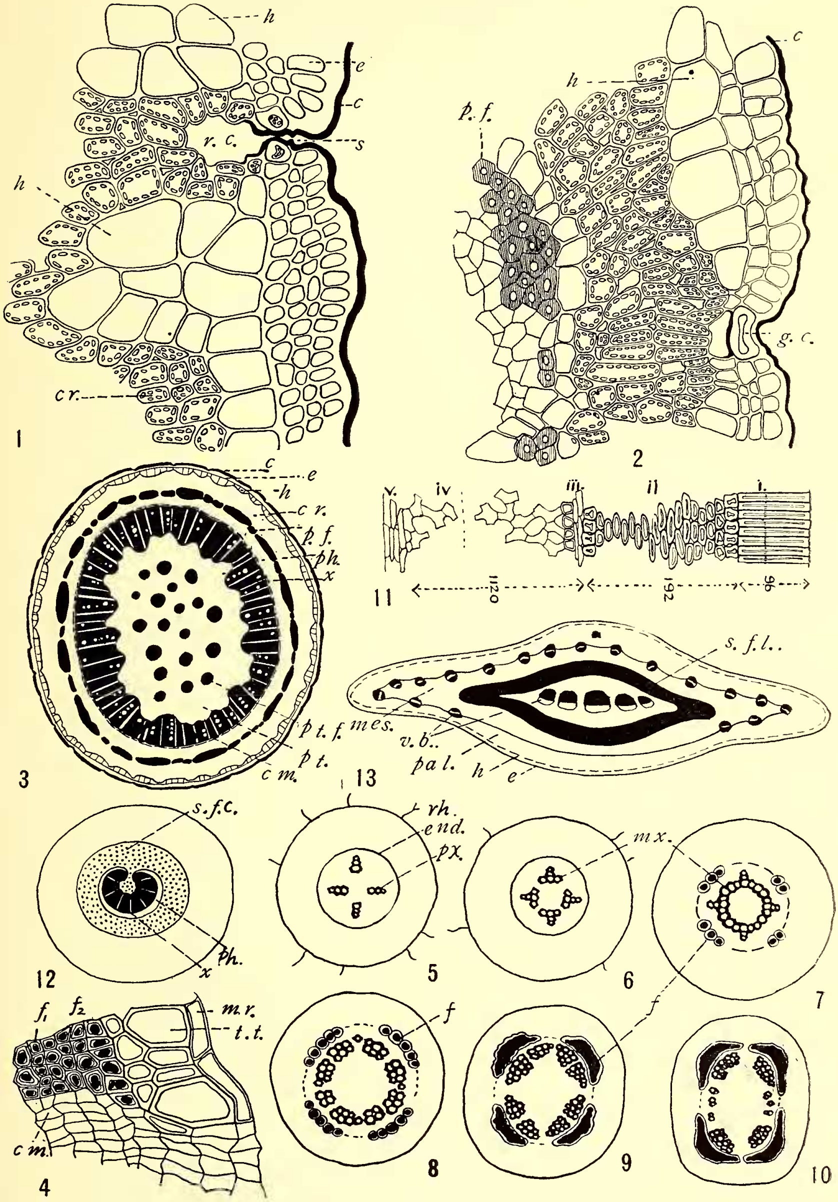

PLATE I. ANATOMY OF CERCIDIUM AND PARKINSONIA.